Chapter 21

Systematic Studies of Madagascar's Endemic Rodents (Muroidea: Nesomyinae): A New Genus and Species from the Central Highlands

Michael D. Carleton and Steven M. Goodman

Abstract

We report a new genus and species of nesomyine rodent from Madagascar's Central Highlands, type locality Antananarivo Province, Manjakatompo, at about 1800 m elevation on the Ankaratra Massif. The form also occurs in upper montane forest within the Réserve Naturelle Intégrale d'Andringitra at 1625 m. The new genus is specifically contrasted to species of *Macrotarsomys,* a taxon that occurs in western Madagascar and is hypothesized to be its closest relative among the seven previously known genera of Nesomyinae. The many generalized features of the new genus provide a basis for renewed examination of the Miocene cricetodontid *Protarsomys* (Kenya, Rusinga Faunal Assemblage); we discount its proposed synonymy with *Macrotarsomys* and question its progenitive significance in regard to the origin of Nesomyinae. The new genus has disjunct populations on the Ankaratra and Andringitra massifs, a distribution that resembles those of numerous other Malagasy organisms restricted to upper montane–sclerophyllous vegetation. This geographical pattern conforms to Humbert's proposed High Mountain Domain.

Résumé

Nous rapportons un nouveau genre et une nouvelle espèce de rongeur nesomyine du haut plateau central de Madagascar, localité du spécimen type Province d'Antananarivo, Manjaka-tompo, vers 1800 m dans le massif de l'Ankaratra. Dans la Réserve Naturelle Intégrale d'Andringitra, cette forme apparaît aussi dans la forêt de montagne à une altitude supérieure à 1625 m. Le nouveau genre se démarque spécifiquement des espèces de *Macrotarsomys,* un taxon qui est distribué à l'ouest de Madagascar et qui est considéré comme le plus proche parmi les sept genres de Nesomyinae connus jusqu'à maintenant. Les nombreuses caractéris-tiques générales de ce nouveau genre fournit une base d'examen pour réexaminer *Protarsomys* (Kenya, Assemblage faunistique de Rusinga) cricetodontid du Miocène; nous ne tenons pas compte de la synonymie proposée avec *Macrotarsomys* et mettons en doute sa valeur compte tenu de l'origine des Nesomyinae. Le nouveau genre présente des populations isolées dans les massifs de l'Ankaratra et de l'Andringitra, une distribution qui ressemble à celle d'autres or-ganismes à la distribution limitée à la végétation sclérophylle des hautes montagnes. Cette distribution géographique est conforme à celle proposée par Humbert pour le Domaine des Hautes Montagnes.

Introduction

The Mission Zoologique Franco-Anglo-Américaine (MZFAA) was a cooperative biological survey of Madagascar conducted from April 1929 to May 1931 (Rand, 1932, 1936). The expedition concentrated its collecting activities on the island's avifauna and, to a lesser extent, on larger mammals such as lemurs (Archbold, 1932; Rand, 1935), and all specimens were approximately evenly divided and deposited among the three participating museums—the Muséum National d'Histoire Naturelle in Paris (MNHN), the British Museum of Natural History in London (BM[NH]) (now called The Natural History Museum), and the American Museum of Natural History in New York City (AMNH). Because of their selective field efforts, the MZFAA teams obtained relatively few examples of Madagascar's endemic rodents, the Nesomyinae (about 70, compared to some 470 lemurs—see Carleton & Schmidt, 1990), but, for the era, the specimens collected represented important additions to our knowledge of the indigenous small mammals. Regrettably, systematists never attempted a critical taxonomic synthesis of the mammalian collections made by the MZFAA, such as was undertaken for the birds (Delacour, 1932; Rand, 1936), and long overlooked was one nondescript, mouse-like rodent obtained by Austin L. Rand near Manjakatompo, a forestry station on the upper slopes of the Ankaratra Massif in the Central Highlands (synonymous with the Central High Plateau).

Recognition of the significance of Rand's capture was further hindered by an innocent processing error, which resulted in receipt of the skin at the AMNH and accession of the skull into the MNHN. For decades, the separated parts of the enigmatic specimen went unnoticed and unappreciated until the early 1970s, when Karl F. Koopman, then Associate Curator in the Department of Mammalogy, AMNH, began an attempt to resolve his inability to classify the lone museum skin according to available taxonomic standards on nesomyine rodents. Subsequent discussions about muroid diagnostic characters with his colleague Guy G. Musser prompted inquiries and led to the eventual rediscovery of the corresponding cranium and mandibles in the MNHN. Through the gracious and understanding cooperation of Dr. Francis Petter, Laboratoire des Mammifères et Oiseaux, MNHN, the errant skull was reunited with its skin in the late 1970s, and the now complete museum specimen (AMNH 100727) only

confirmed Koopman's suspicions of its morphological uniqueness and newness to the rodent fauna of Madagascar. Other research commitments and priorities intervened to divert the attention of Koopman and Musser from jointly describing the new taxon.

The impetus to report Rand's Manjakatompo specimen at this time and in the present context issues from renewed interest in the native rodents of Madagascar and from the resurgence of fieldwork on the island. Ongoing revisionary work by Carleton (1994) and Carleton and Schmidt (1990), and the 1993 rediscovery by Goodman of Rand's unremarkable mouse on the Andringitra Massif, over 300 km to the south of Ankaratra, make formal identification of this form both propitious and necessary. The fresh material from the Réserve Naturelle Intégrale (RNI) d'Andringitra encourages fuller elaboration of the form's defining traits, which further attest to the distinctiveness of the taxon and convince us that it represents a genus and species new to the fauna of Madagascar.

Materials and Methods

The material described herein and the comparative series of *Macrotarsomys* that are referenced are housed in the AMNH, New York City; the Field Museum of Natural History (FMNH), Chicago; the MNHN, Paris; the National Museum of Kenya (KNM), Nairobi; and the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C. Nesomyine holdings in other museums have been studied by M.D.C., and one or both authors have examined the holotypes of all described forms of Nesomyinae, except for Peters's (1870) *Nesomys rufus*. The following samples, consisting of conventional round skins with skulls, as well as complete skeletons and fluid-preserved whole carcasses, were consulted for the various tabular summaries and anatomical comparisons.

Macrotarsomys bastardi bastardi—Fianarantsoa Province: 35 mi (= 56 km) N Ihosy, 3000 ft (= 915 m) (AMNH 119710); 5 km E Route Nationale 7, along road to Ivohibe, 750 m (USNM 328793–328807).

Macrotarsomys bastardi occidentalis—Mahajanga Province: 40 km S Marovoay, Ampijoroa (USNM 341817–24). Toliara Province: 40 km N Morondava, 7 km from sea, Beroboka (AMNH

119708–9); Petriky Forest, 5–7 km SE Manambaro, 20 m (USNM 578715–9 and 578822–3).

Macrotarsomys ingens—Mahajanga Province: Ankarafantsika Reserve, Ampijoroa (MNHN 1958.636 and 1961.214–5; USNM 328831 and 576753).

Protarsomys macinnesi—Lower Miocene, Rusinga Faunal Assemblage, Kenya (cast of holotype, KNM 2350, cranium with associated mandibles); Lower Miocene, Legetet, Kenya (cast of a referred lower jaw with m1-3, KNM 2188).

Six measurements, in millimeters (mm) or grams (g), were taken by S.M.G. for each FMNH specimen in the flesh. Their abbreviations and definitions are given below.

TOTL, total length of body and tail: from the tip of the nose to the end of the caudal vertebra (not including terminal hair tuft).

HBL, head and body length: from the tip of the nose to the distalmost point of the body (at base of tail).

TL, tail length: from the base of the tail (held at right angles to the body) to the end of the last caudal vertebra (not including terminal hair tuft).

HFL, hind food length: from the heel to the tip of the longest toe (not including claw).

EL, ear length: from the basal notch to the distalmost rim of the pinna.

WT, weight in grams: measured with Pesola spring scales to ± 0.5 g.

Sixteen cranial and two dental dimensions were measured by M.D.C. to the nearest 0.1 mm using handheld digital calipers accurate to 0.03 mm. These measurements, and their abbreviations, follow the anatomical landmarks defined and illustrated in Carleton (1994): BBC, breadth of the braincase; BIF, breadth of incisive foramina; BM1s, breadth of the bony palate across the first upper molars; BOC, breadth across the occipital condyles; BR, breadth of rostrum; BZP, breadth of the zygomatic plate; DAB, depth of the auditory bulla; IOB, interorbital breadth; LBP, length of bony palate; LD, length of diastema; LIF, length of the incisive foramina; LM1-3, coronal length of maxillary toothrow; LR, length of rostrum; ONL, occipitonasal length; PPB, posterior breadth of the bony palate; PPL, postpalatal length; WM1, width of the first upper molar; and ZB, zygomatic breadth.

Analytical routines for the standard descriptive statistics were carried out using the Systat (version 5.05, 1994) computer program. Morpholog-ical terms generally follow Carleton (1980) and Voss (1988); names of dental structures follow Reig (1977), as illustrated by Carleton and Musser (1989). Field methods for the three FMNH specimens originating from the RNI d'Andringitra are described in Chapter 22.

Monticolomys, new genus

Type Species—*Monticolomys koopmani,* described below as new.

Diagnosis—A form of the murid rodent subfamily Nesomyinae (sensu Carleton & Musser, 1984; Musser & Carleton, 1993) characterized by: small size (TOTL = 205–240 mm; HBL = 89–101 mm) (in other nesomyines except *Eliurus minor* and *Macrotarsomys bastardi*, HBL ≥ 130 mm); short (15–18 mm), densely furred, and rounded pinnae (pinnae long, ≥ 21 mm, and sparsely haired in *Macrotarsomys*); tail appreciably longer than head and body together, about 135–140% of HBL (TL ≤ HBL in *Brachyuromys, Gymnuromys, Hypogeomys,* and *Nesomys*), without noticeable elongation of caudal hairs over distal half (distal tip penicillate in *Macrotarsomys,* a brushy tuft in *Eliurus*); hind foot relatively long and broad, outer digits I and V comparatively long (hind foot narrow, outer digits relatively short in *Macrotarsomys*); plantar surface with six fleshy pads, thenar and hypothenar as large as interdigital pads (thenar and hypothenar diminutive in *Macrotarsomys*); ungual tuft well developed, surpassing tip of claw (tuft hairs shorter than claw in *Macrotarsomys*).

Cranium small (ONL = 26–28 mm, LM1-3 = 3.5–3.7 mm) and delicately built with slender, parallel-sided zygomatic arches and narrow, hourglass-shaped interorbit; vascular groove on squamosal-alisphenoid, stapedial and sphenofrontal foramina present (groove and foramina lacking in *Brachytarsomys, Brachyuromys, Eliurus, Gymnuromys,* and *Hypogeomys*); alisphenoid strut absent (strut present in *Brachyuromys,* most *Eliurus, Hypogeomys,* and *Nesomys*); ectotympanic bullae moderately inflated, narrow ventromedial wedge of periotic exposed (bullae smaller, wide expanse of periotic visible in *Brachytarsomys, Eliurus,* and *Gymnuromys*; bullae notably larger, periotic mostly obscured in *Brachyuromys, Hypogeomys, Macrotarsomys,* and *Nesomys*); tegmen tympani reduced, not contacting squamosal (articulation with squamosal in *Brachytarsomys, Eliurus,* and *Gymnuromys*).

Upper toothrows divergent anteriorly (convergent anteriorly in *Brachyuromys,* more or less parallel in *Brachytarsomys, Eliurus, Gymnuromys, Hypogeomys,* and *Nesomys*); molars cuspidate and brachyodont (cheek teeth moderately to extremely hypsodont, cuspation lost or indistinct, and occlusal surface planar in *Brachyuromys, Brachytarsomys, Eliurus, Gymnuromys,* and *Hypogeomys*); mesolophs(ids) absent, posterolophs rudimentary, anteroconids imperfectly developed (mesolophs[ids] present in *Gymnuromys* and *Nesomys*); lower third molar reduced, notably smaller than second molar (size of third molar approximately equal to second in *Brachyuromys, Eliurus, Hypogeomys,* and *Nesomys*; conspicuously larger than second molar in *Gymnuromys*); upper molars with three roots and lower molars with two (upper molars four-rooted in *Hypogeomys*).

MORPHOLOGICAL DESCRIPTION—As for the single known species, described below.

Monticolomys koopmani, new species
(Figs. 21-1 to 21-5; Tables 21-1 and 21-2)

HOLOTYPE—AMNH 100727: skin and skull of young adult male; original no. 62, collected May 24, 1929, by Austin L. Rand as part of the MZFAA (see Rand, 1932, 1936).

Standard measurements (in mm) from the specimen tag attached to the skin of the type include: total length, 205; tail length, 116; hind foot length, without claw, 24 (dry hind foot length, as measured by M.D.C. with claw, is 25.5); and ear length, 15.

The condition of the skin is good. The skull is damaged, with its right bullae detached and present in the vial, both zygomatic arches incomplete, and the orbitosphenoid walls on both sides broken; the mandibles are separated, and their angular and coronoid processes are incomplete.

TYPE LOCALITY—Madagascar, Antananarivo Province, Manjakatompo, ca. 19°20′S 47°26′E.

Rand identified the locality only as "Monjakatompo" (spelling in the United States Board on Geographic Names, 1989 gazetteer, as Manjakatompo) on his original tag and later (1936) supplied the collection elevation as 1800 m. This height probably refers to an area of fragmented natural forest intermixed with secondary grassland in the vicinity of the forestry station of Manjakatompo. Elevational records mentioned on other specimen tags or in Richard Archbold's journal (AMNH Mammalogy Department) indicate that the team worked the slopes of Ankaratra at least from 1650 m to 1950 m (Rand's own field notes for the MZFAA were apparently lost or destroyed). The little natural forest remaining on the slopes of Ankaratra above Manjakatompo is estimated to be about 650 ha (Nicoll & Langrand, 1989).

REFERRED SPECIMENS—FMNH 151727 (male, skull with postcranial skeleton), 151899 (female, skull with whole carcass in fluid), and 151900 (male, skull with whole carcass in fluid); all from Fianarantsoa Province, 38 km S Ambalavao, RNI d'Andringitra, ridge E of Volotsangana River, 1625 m; 22°11′S 46°58′E; collected by S.M.G., December 12–14, 1993.

DISTRIBUTION—At present known only from two localities in the Central Highlands, about 1800 m on the Ankaratra Massif and 1625 m on the Andringitra Massif.

DIAGNOSIS—As for the genus, above.

MORPHOLOGICAL DESCRIPTION—Fur soft, relatively thick and fine (based on the holotype, AMNH 100727). Cover hairs of dorsum usually tricolored—basal two-thirds plumbeous gray, middle band a deep ochraceous, and short tip dark brown to black; guard hairs entirely black, longer, and more heavily concentrated toward the middorsum and on the rump; general appearance of upperparts a somber or muted dark brown. Fur over inguinum, abdomen, and chest with plumbeous bases and pale buffy to whitish tips, mostly white to bases on chin and throat; combined effect a dark gray ventrum not sharply demarcated from dorsum. Mystacial vibrissae medium in length, the longest whiskers reaching the top of the pinnae when appressed to the skin. Pinnae short and rounded (Fig. 21-1; Table 21-1), densely clothed internally and externally with slate hairs. Tail very long relative to head-and-body length (TL about 138% of HBL) and appearing

---

←

FIG. 21-1.   Dorsal and ventral views of round museum skins: **left pair,** the holotype of *Monticolomys koopmani* (AMNH 100727, TOTL = 205 mm), a young adult male from Antananarivo Province, Manjakatompo; **right pair,** an original topotype of *Macrotarsomys bastardi occidentalis* (AMNH 119709, TOTL = 228 mm), an adult male from Toliara Province, Beroboka.
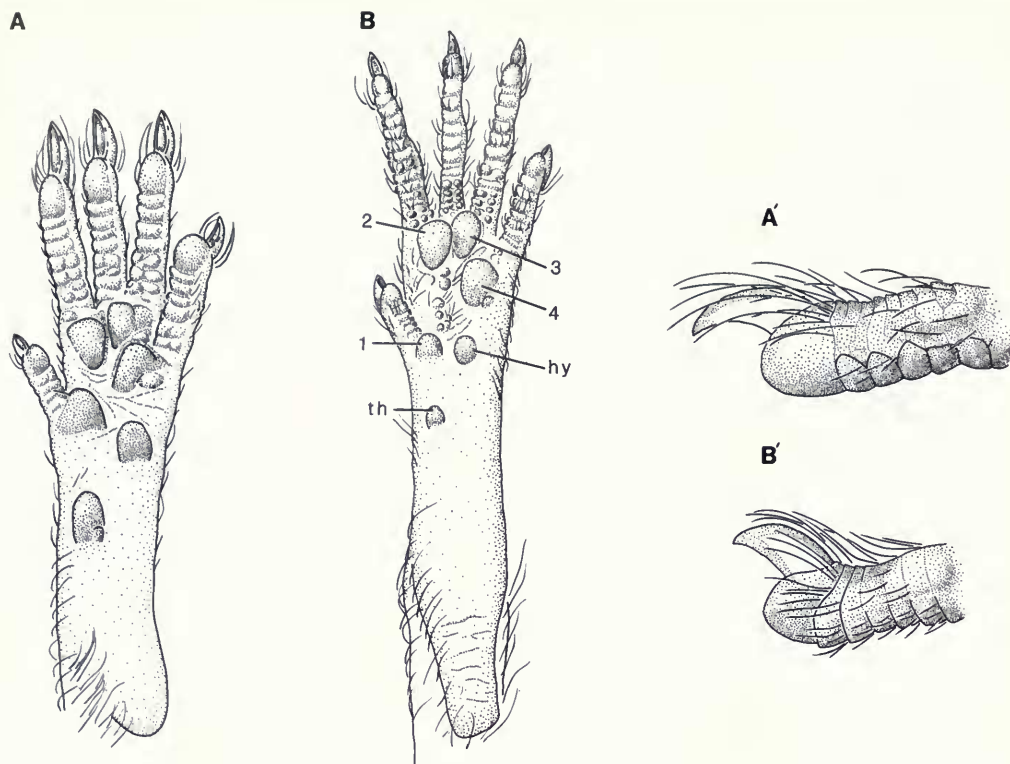
Fig. 21-2. Plantar view of the left hind foot and lateral view of the distal phalanges of the fourth digit: **A–A′**, *Monticolomys koopmani* (FMNH 151900, HFL = 25 mm), an adult female from Fianarantsoa Province, RNI d'Andringitra; **B–B′**, *Macrotarsomys bastardi* (USNM 578822, HFL = 27 mm), an adult male from Toliara Province, Petriky Forest. Abbreviations: 1–4, interdigital pads one through four; hy, hypothenar pad; th, thenar pad. Note the contrasts in size and position of the plantar pads between *Monticolomys* (A) and *Macrotarsomys* (B), greater pilosity on the undersurface of the phalanges in *Macrotarsomys* (B′), and stronger development of the ungual tuft in *Monticolomys* (A′).

monocolored; caudal hairs a pale brown, medium in length over entire tail without notable penicillation or development of distal tuft; scutellation fine, partially obscured by tail hairs. Mammae number six (based on FMNH 151899), distributed as postaxial, abdominal, and inguinal pairs.

Tops of metapodials and phalanges covered with fine white hairs; ungual tufts present, the white hairs extending beyond end of claw (Fig. 21-2); palmar and plantar surfaces and underneath of phalanges naked. Forefoot with stubby pollex bearing a nail, other manual digits with claws. Hind foot relatively long (Table 21-1), about 25% of HBL, and wide, with claws on all digits. Central digits (II–IV) of hind foot almost as long as corresponding metatarsals; digit V relatively long, its claw reaching to end of second phalanx of digit IV; digit I more reduced, its claw extending to middle of first phalanx of digit II (Fig. 21-3).

Plantar surface bearing six moderately sized and cushion-like pads (Fig. 21-2); interdigital pads 2–4 set close together at base of digits, interdigital 1 situated somewhat apart at base of hallux; hypothenar pad about as large as interdigitals, positioned near to but slightly posterior of interdigital 1; thenar ovate, situated near middle of tarsus-metatarsus, and subequal in size to distal pads (Fig. 21-2).

Cranium lightly constructed, delicate in appearance (Fig. 21-4). Rostrum narrow and moderately long, about 35% of ONL, taper forward from nasolacrimal capsules to end of nasals very gradual; anterior tips of nasals rounded, posterior margins blunt and coextensive with posteriormost limit of rostral processes of premaxillae. Zygomatic plate narrow, its anterior edge slightly convex and set well behind nasolacrimal capsule; posterior border of plate positioned appreciably in front of anterior root of M1; dorsal notch distinct
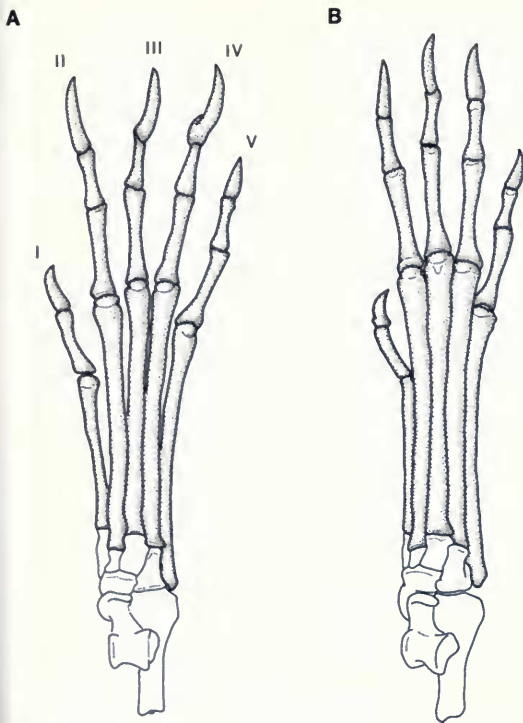
236

FIG. 21-3. Dorsal view of the right hind foot skeleton: **A,** *Monticolomys koopmani* (FMNH 151727, HFL = 24 mm), an adult male from Fianarantsoa Province, RNI d'Andringitra; **B,** *Macrotarsomys bastardi* (USNM 578719, HFL = 28 mm), an adult male from Toliara Province, Petriky Forest. Abbreviations: I–V, pedal digits one through five. Note the relatively greater lengths of digits I and V in *Monticolomys* as compared to those of *Macrotarsomys,* as well as the tighter coalignment of the metatarsals in *Macrotarsomys.*

but shallow. Zygomatic arches thin and parallel-sided to slightly bowed over midportion, projecting laterad just beyond margins of braincase and weakly converging anteriorly; jugal slender but relatively long, forming most of midspan of arch and distinctly separating zygomatic processes of squamosal and maxillary.

Interorbital region narrow, exposing floor of orbits in dorsal view; hourglass-shaped, lacking supraorbital shelving and ridging; orbital projection of lacrimal inconspicuous. Braincase similarly free of ridges and crests, smooth and rounded in dorsal appearance (Fig. 21-4); frontoparietal suture evenly curved, not defining a sharp angle at midsagittal juncture; interparietal moderately large and rhomboidal in outline, its lateral apices not contacting squamosals; dorsal profile of skull gently arched throughout, its highest point formed just anterior to the frontoparietal junction.

Incisive foramina medium in length, spanning about 66% of diastema and terminating at level of anterior root of first molars. Palatal bridge relatively broad and smooth, devoid of corrugations and excrescences; posterior palatine foramina occur as simple round holes in maxillopalatine suture, about level with abutment of M1-m2; posterior border of palate U-shaped, situated even with end of third molars, and lacking posterolateral palatal pits. Lateral borders (pterygoid processes) of mesopterygoid fossa more or less straight sided and enclosing spacious sphenopalatine vacuities. Parapterygoid fossae broad compared to width of mesopterygoid fossa, relatively short and triangular in shape, recessed little relative to the plane of the hard palate; roof of parapterygoid fossae almost flat and mostly osseus, pierced only by posterior opening to alisphenoid canal near their posterolateral corner and there scored by a groove for passage of the infraorbital branch of the stapedial artery.

Ectotympanic bullae moderately sized, with narrow posteromedial wedge of the periotic visible in ventral aspect; anterodorsal rim of the bulla abuts the ventrolateral margin of the squamosal bone but not obscuring the slit-like middle lacerate foramen; anterior flange of tegmen tympani inconspicuous, not contacting ventrolateral margin of squamosal; eustacian tube short, overlapping but not enveloping tip of pterygoid process; malleus of the parallel type, orbicularis apophysis knob-like without definitive neck, deflected ventromedially. Postglenoid foramen large, semioval in outline, circumscribing an area about three to four times that of the smaller subsquamosal fenestra; hamular process of squamosal well defined and slender. Mastoid capsule small and bulbous, perforated by posterodorsal fontanelle.

Alisphenoid strut absent, masticatory-buccinator and accessory oval foramina conjoined as one expansive opening. Sphenofrontal and stapedial foramina present, squamosal-alisphenoid groove well defined, posterior opening of alisphenoid canal large, and vascular groove crossing the posterolateral corner of the parapterygoid plate—anatomical landmarks suggesting a complete cephalic circulatory pattern with retention of the supraorbital and infraorbital branches of the stapedial artery.

Coronoid process of dentary falcate, extending dorsad slightly above the condylar process; sigmoid and angular notches clearly incised but unremarkable in size and shape; alveolus of lower incisor terminates posteriorly at level of coronoid
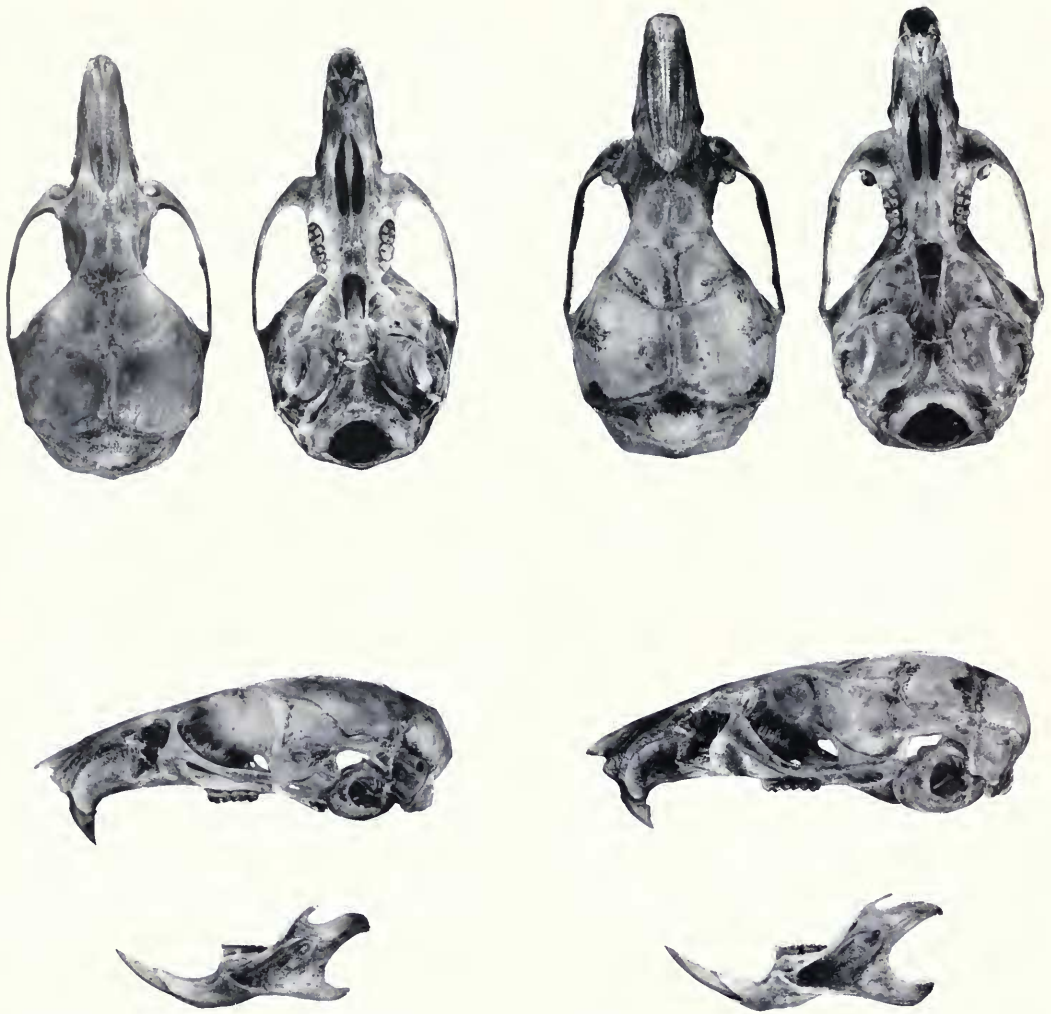
Fig. 21-4. Dorsal, ventral, and lateral views (×2) of the cranium and mandible: **left,** *Monticolomys koopmani* (FMNH 151899, ONL = 28.1 mm), an adult female from Fianarantsoa Province, RNI d'Andringitra; **right,** *Macrotarsomys bastardi* (USNM 578715, ONL = 29.3 mm), an adult female from Toliara Province, Petriky Forest.

process, well below ventral rim of sigmoid notch; capsular process evident as low mound.

Axial skeleton (per one specimen, FMNH 151727) with 13 thoracic, seven lumbar, four sacral (two pseudosacral), and 38 caudal vertebrae; tuberculum of first rib articulates only with transverse process of first thoracic vertebra, not touching transverse process of seventh cervical; neural spine of second thoracic vertebra rises conspicuously above the spines of other thoracics. Entepicondylar foramen present on humerus.

Upper incisors asulcate and opisthodont; enamel medium orange. Upper molar rows divergent anteriorly; upper and lower second molars about three-quarters the size of the first molars but similar in occlusal design; upper and lower third molars notably smaller, circular to oval, about one-half to two-thirds the length and area of the contiguous second molars, and their serial homologies more obscure. Molars decidedly brachyodont, cuspidate (Fig. 21-5); principal cusps positioned nearly opposite in the upper molars, more alternate in the lowers. Anterocone of M1 well defined, broad and undivided (weakly bilobate in one specimen); anteroconid of m1 hardly distinguishable from metaconid and anterior cingulum; entoconid poorly defined on m3; low median mure(id) interconnects anterior and posterior pairs

Fig. 21-5. Occlusal views (×20) of the upper (left member) and lower (right member) right molar rows: **left pair,** *Monticolomys koopmani* (FMNH 151899, LM1-3 = 3.42 mm), an adult female from Fianarantsoa Province, RNI d'Andringitra; **right pair,** *Macrotarsomys bastardi* (USNM 578715, LM1-3 = 3.95 mm), an adult female from Toliara Province, Petriky Forest.

of cusps on each first and second molar. Principal lingual and labial enamel folds broad and meet near the midline of the tooth, not interpenetrating; posteroloph (postcingulum) of M1-2 and corresponding posteroflexus indistinct, obliterated after slight wear; posterolophid and broad posteroflexid present and persistent with wear on m1-2, indistinct or absent on m3; protoflexus of M2 absent, anteroloph and paraflexus short; metaflexid of m1 represented by faint indentation or indiscernible, opposite protoflexid well defined; anterolabial cingulum present but small on m2, variable on m3; mesolophs(ids), as well as other accessory crests and styles, absent. Three roots on each upper molar and two on each lower.

NOTES ON NATURAL HISTORY—The habitat where Rand collected the type is characterized on the skin specimen tag as "grass slope with scattered bushes." The type specimen, even at the time of the MZFAA in 1929, likely originated from despoiled habitat. In his later summary of the itinerary, Rand (1936: pp. 161 and 163) expanded upon the vegetation of Ankaratra:

The slopes of the greater part of the mountain were grass-covered and supported a growth of health and bracken . . . just above Monjakatompo, was an area of humid forest, an isolated remnant of the forest that once covered the central portion of Madagascar. This wooded area was of the humid forest type, with large trees hung with lianas and mosses. Tree ferns were common and in some places there was considerable undergrowth.

Populations of *Monticolomys koopmani* may co-occur with a variety of other nesomyine species. On Ankaratra, Rand also collected three specimens of *Brachyuromys betsileoensis* (AMNH 100802, BMNH 35.1.8.341, and MNHN 1932.3521) near Manjakatompo, at 1700 m and 1950 m. The spare habitat annotations on their skin specimen tags ("grass and brush at edge of pond"; "grass and brush ridge") leave open the question of whether the *Brachyuromys* were syntopic with *Monticolomys*. The grasslands on the mountain are not natural vegetation formations but have resulted from human-set fires (Perrier de la Bâthie, 1927; Nicoll & Langrand, 1989). To judge from the personal field notes of Richard

TABLE 21-1. Selected external and craniodental measurements (in mm) of the holotype (AMNH 100727) and referred specimens (FMNH 151727, 151899, and 151900) of *Monticolomys koopmani*.

Variable	Holotype (Ankaratra Massif)	Referred specimens (Andringitra Massif)
TOTL	205.0	236.3 (234–240)
HBL	89.0	98.0 (94–101)
TL	116.0	138.0 (134–143)
HFL	24.0	24.3 (24–25)
EL	15.0	18.3 (18–19)
WT	⋯	26.3 (25–27)
ONL	26.3	27.8 (27.5–28.1)
ZB	⋯	13.6 (13.1–14.1)
BBC	12.5	12.7 (12.4–13.2)
IOB	3.9	4.0 (3.9–4.0)
LR	8.5	9.9 (9.6–10.2)
BR	4.2	4.7 (4.5–4.9)
PPL	8.7	9.5 (9.3–9.7)
LBP	3.7	4.2 (4.0–4.4)
LIF	5.3	5.2 (5.1–5.3)
BIF	2.0	2.0 (1.9–2.0)
LD	7.2	7.9 (7.7–8.0)
BM1s	5.7	5.9 (5.8–6.0)
DAB	4.4	4.8 (4.7–4.9)
BZP	2.2	2.2 (2.1–2.2)
BOC	6.4	6.6 (6.5–6.8)
LM1-3	3.7	3.5 (3.4–3.7)
WM1	1.1	1.1 (1.0–1.1)

Refer to the Materials and Methods section for an explanation of the abbreviations.

Archbold, who accompanied Rand to Ankaratra and also collected around Manjakatompo, populations of *Rattus rattus* were well established in the area at the time.

The more thorough survey conducted within the RNI d'Andringitra documents sympatry of *Monticolomys koopmani* with seven other rodent species—*Rattus rattus, Brachyuromys ramirohitra, Eliurus majori, E. minor, E. tanala, Gymnuromys roberti,* and *Nesomys rufus* (voucher numbers are listed in Chapter 22). Several of these Nesomyinae are themselves restricted to montane and upper montane vegetational zones (*Brachyuromys ramirohitra, Eliurus majori, E. tanala,* and *Nesomys rufus*) or are widely ranging in altitudinal occurrence (*Eliurus minor* and *Gymnuromys roberti*).

The specimens from Andringitra were collected in upper montane forest (ridge-top sclerophyllous forest) that is regularly shrouded in mist and cloud cover. The area (Fig. 21-6) is dominated by dense bamboo stands of the genera *Arundinaria* and *Nastus* and by trees of the families Podocarpaceae, Cunoniaceae, and Pandanaceae (Chapter 2). For woody plants over 10 cm diameter at breast height (dbh), trees in the 1625 m zone averaged 17.0 cm dbh and 7.9 m tall (Chapter 4). Furthermore, at this elevation, there was a marked increase in epiphytes, mosses, and lichens in tree crowns and on trunks in comparison to forests at lower elevations.

The relatively long tail, the conformation of the hind foot, and the large plantar pads suggest that individuals of *Monticolomys* are adept climbers. In the RNI d'Andringitra, both live-caught specimens (FMNH 151899 and 151900) were captured on successive nights in the same Sherman trap placed on a nearly horizontal segment of a liana that was less than 5 cm in circumference and 2 m above the ground. The vine originated at the ground and wound its way to the canopy. The third specimen (FMNH 151727) was found the next morning in a pitfall bucket along with two *Microgale taiva* (FMNH 151724 and 151725). With just three records, little can be said about the species' focus of activity, whether predominantly arboreal, scansorial, or terrestrial.

The two males from Andringitra, collected in December 1993, possessed partially or fully descended testes; the one female had small teats and an imperforate vagina.

REMARKS—The natural environments on the Ankaratra and Andringitra massifs inhabited by *Monticolomys* are isolated, their unique montane populations wholly allopatric to one another (see discussion on biogeography below and Fig. 21-11). The meager sample sizes available from the type locality (N = 1) and from the RNI d'Andringitra (N = 3) hinder any meaningful evaluation of the level of differentiation between the two distantly separated localities. Bias in age representation further complicates appreciation of intra- and interlocality differences—the holotype is a young adult male, his molars little worn but in mature pelage, whereas the three paratypes (two males, one female) are fully adult with moderately to heavily worn toothrows.

Age-related, post-weaning growth may plausibly account for the generally smaller size of the holotype as compared to the three Andringitra specimens (Table 21-1). Certain mensural variables—such as HBL, TL, ONL, LR, LD, PPL, all of which are decidedly shortest in the holotype—may exhibit substantial age effects among the samples typically available to the systematist, even with attempts to control for age biases by eliminating juveniles or restricting analyses to

TABLE 21-2. Comparison of selected external and craniodental measurements (in mm) of *Monticolomys koopmani* and species of *Macrotarsomys*. Statistics for the samples include the mean ± standard deviation, and the range.

Variable	*Monticolomys koopmani* (N = 4)	*Macrotarsomys b. bastardi* (N = 9)	*Macrotarsomys b. occidentalis* (N = 4)	*Macrotarsomys ingens* (N = 4)
TOTL	228.5 ± 15.9 205.0–240.0	213.0 ± 11.7 195.0–232.0	225.5 ± 10.8 213.0–235.0	336.5 ± 36.6 310.0–390.0
HBL	95.7 ± 5.4 89.0–101.0	91.6 ± 3.2 86.0–95.0	96.7 ± 4.2 92.0–102.0	127.0 ± 15.7 115.0–150.0
TL	132.5 ± 1.16 116.0–143.0	121.5 ± 12.1 100.0–142.0	128.7 ± 6.9 121.0–136.0	209.5 ± 21.7 193.0–240.0
HFL	24.3 ± 0.5 24.0–25.0	24.6 ± 0.9 23.0–26.0	26.7 ± 1.0 26.0–28.0	35.3 ± 2.5 32.0–38.0
EL	17.5 ± 1.7 15.0–19.0	21.3 ± 1.2 20.0–23.0	23.0 ± 1.6 21.0–25.0	24.3 ± 1.5 23.0–26.0
WT	26.3 ± 1.2 25.0–27.0	24.5 ± 2.7 21.0–28.0	31.0 ± 5.6 26.0–38.0	57.0 54.0, 60.0
ONL	27.4 ± 0.8 26.3–28.1	28.1 ± 0.7 26.7–28.9	28.6 ± 0.5 28.2–29.3	38.9 ± 2.5 35.4–41.3
ZB	13.6 ± 0.5 13.1–14.1	14.0 ± 0.5 13.0–14.6	14.5 ± 0.4 14.1–14.8	18.9 ± 1.5 16.7–20.2
BBC	12.7 ± 0.4 12.4–13.2	11.3 ± 0.2 10.9–11.5	11.7 ± 0.3 11.3–12.1	14.3 ± 0.5 13.5–14.3
IOB	3.9 ± 0.1 3.9–4.0	4.6 ± 0.1 4.3–4.7	4.8 ± 0.1 4.6–4.9	5.6 ± 0.4 5.1–6.0
LR	9.5 ± 0.7 8.5–10.2	10.2 ± 0.5 9.5–11.1	10.1 ± 0.3 9.9–10.5	14.4 ± 1.2 13.0–16.0
BR	4.5 ± 0.3 4.2–4.9	4.7 ± 0.2 4.4–5.1	4.9 ± 0.2 4.7–5.2	6.8 ± 0.3 6.6–7.1
PPL	9.3 ± 0.4 8.7–9.7	9.5 ± 0.4 9.1–10.0	9.8 ± 0.6 9.1–10.3	13.3 ± 1.1 11.9–14.6
LBP	4.1 ± 0.3 3.7–4.4	4.7 ± 0.2 4.4–4.9	4.6 ± 0.3 4.2–4.9	6.3 ± 0.5 5.6–6.9
LIF	5.2 ± 0.1 5.1–5.3	5.1 ± 0.2 4.9-5.5	5.0 ± 0.3 4.7–5.4	7.1 ± 0.4 6.7–7.5
BIF	2.0 ± 0.1 1.9–2.1	2.0 ± 0.1 1.8–2.1	2.1 ± 0.2 1.9–2.3	2.6 ± 0.2 2.4–2.8
LD	7.7 ± 0.3 7.2–8.0	7.4 ± 0.4 6.8–8.0	7.7 ± 0.2 7.5–7.9	11.6 ± 0.9 10.3–12.5
BM1s	5.9 ± 0.1 5.7–6.0	5.9 ± 0.2 5.5–6.2	5.9 ± 0.1 5.7–5.9	7.7 ± 0.5 7.0–8.0
DAB	4.7 ± 0.3 4.4–4.9	5.5 ± 0.2 5.1–5.7	5.4 ± 0.1 5.2–5.5	7.0 ± 0.6 6.3–7.5
BZP	2.2 ± 0.05 2.1–2.2	2.9 ± 0.2 2.6–3.1	2.8 ± 0.1 2.7–2.9	3.8 ± 0.2 3.5–4.0
BOC	6.5 ± 0.2 6.4–6.8	6.1 ± 0.3 5.6–6.3	6.5 ± 0.2 6.3–6.7	8.4 ± 0.6 7.7–8.9
LM1–3	3.57 ± 0.12 3.42–3.70	4.08 ± 0.17 3.79–4.31	3.91 ± 0.05 3.85–3.95	4.85 ± 0.16 4.71–5.04
WM1	1.09 ± 0.02 1.07–1.12	1.28 ± 0.06 1.21–1.39	1.19 ± 0.02 1.17–1.21	1.64 ± 0.04 1.59–1.68

specimens assigned to crudely defined age–tooth-wear categories (Voss & Marcus, 1992). We note that several cranial dimensions measured across the brain (BBC, IOB, BOC) or on the molars LM1-3, WM1), regions that change little or not at all with age following weaning, are basically alike in the Ankaratra and Andringitra examples (Table 21-1).

In view of such insufficiencies in sample size and imbalanced age representation, and lacking other evidence of substantial divergence, we treat the two allopatric samples as one species but stress the need for additional voucher material. Broader age series are especially critical to verify the typical condition of traits such as the presence of a posteroloph and formation of the anteroconid.

FIG. 21-6. View through the understory of upper montane forest at 1625 m on the eastern slopes of the RNI d'Andringitra. Portions of this forest, where three specimens of *Monticolomys koopmani* were taken during the 1993 inventory, are dominated by dense stands of bamboo (*Arundinaria* and *Nastus*), intermixed with *Podocarpus* trees. The groundcover is largely covered by *Pandanus* (Photo by C. J. Raxworthy).

These dental characters are obliterated after slight trituration and are best observed in juvenile specimens.

ETYMOLOGY—The generic name, mountain-dwelling mouse, evokes the montane occurrence of the form. The species is named to honor the

lifelong systematic contributions of Karl F. Koopman, Curator Emeritus in the Department of Mammalogy, AMNH, and one-time Assistant Curator of Mammals, FMNH. His curiosity, piqued by the orphaned skin that would not key out properly according to the standard classification, led

him to the perception that it indeed represented a fundamentally different kind of Malagasy rodent.

Morphological Comparisons

Individuals of *Monticolomys koopmani* are immediately distinguishable from other kinds of Nesomyinae on the basis of their diminutive size and generalized murine appearance. The mouse-like form offers sharp visual contrast to the distinctive and highly divergent physiognomies of the much larger *Brachytarsomys*, *Brachyuromys*, *Gymnuromys*, *Hypogeomys*, and *Nesomys* (for example, see descriptions, measurements, and/or keys in Ellerman, 1941, 1949; Petter, 1972, 1975; and Chapter 22, this work). Among the tufted-tailed rats, genus *Eliurus*, only specimens of *E. minor* approach those of *Monticolomys* in overall size. Although comparable in average total length, individuals of *Monticolomys* possess a still lighter build, shorter head-and-body length, relatively longer tail, and longer hind feet (see Carleton, 1994; and Chapter 22, Table 22-2). Furthermore, they lack the conspicuous "bottle-brush" tail that characterizes *E. minor* and other species of *Eliurus*. Crania and dentitions of *E. minor* and *Monticolomys* differ even more strikingly than external form and permit no confusion of the two (see Carleton, 1994).

Although discrimination of *Monticolomys* from most nesomyines is straightforward, two genera, one living and one extinct, present less-pronounced contrasts and raise broader questions of phylogenetic relationship. One, *Macrotarsomys*, whose gerbil-like physique may suggest very distant phyletic association, in fact resembles *Monticolomys* quite closely in certain cranial and dental details that require critical elaboration. The other, the Miocene form *Protarsomys*, merits attention because some authors have viewed it as close to the ancestry of Madagascar's indigenous rodents (Lavocat, 1973, 1978), if not actually synonymous with extant *Macrotarsomys* (Chaline et al., 1977; Petter, 1990).

Comparison with *Macrotarsomys* Milne Edwards and G. Grandidier

The following morphological descriptions and comparative accounts are based on the four examples of *Monticolomys koopmani* and specimens representing both *Macrotarsomys bastardi* (including *M. occidentalis* Ellerman, 1949) and *M. ingens* (see Materials and Methods section). The type species of *Macrotarsomys*, *M. bastardi* Milne Edwards and G. Grandidier (1898), differs in subtle aspects from the later named and physically much larger congener *M. ingens* (Petter, 1959); however, unless noted otherwise, contrasts to *Monticolomys* apply to both species of *Macrotarsomys*.

PELAGE AND EXTERNAL FORM—The dark brown dorsum and dull gray ventrum of *Monticolomys* present a somber impression compared to the light sandy to clay brown upperparts and wholly white underparts of *Macrotarsomys*. Lateral demarcation of the dorsal-ventral pelage is thus conspicuous in the latter genus. Pelage texture is similarly fine in both genera, but appears longer and denser, for the size of the animal, in the sample of *Monticolomys*.

The generalized murine appearance of *Monticolomys* offers several points of contrast to the gerbilline form that characterizes *Macrotarsomys* (Fig. 21-1). The pinnae of *Monticolomys* are small, thick, and rounded, protruding only slightly above the body fur, and densely cloaked with black hairs. Those of *Macrotarsomys*, however, are much longer and wider (Table 21-2), appearing almost naked (clothed with fine white hairs internally and pale brown externally) and more pliant. The tails of both *Monticolomys* and *Macrotarsomys bastardi* are relatively long (TL 133–138% of HBL), that of *M. ingens* exceptionally so (TL 160% of HBL). Examples of *Monticolomys*, however, lack the distal elongation of caudal hairs forming a modest pencil; instead the hairs are roughly even in length, spanning about two caudal annuli, over the entire tail. In specimens of *Macrotarsomys*, hairs covering the proximal two-thirds of the tail are sparse and short, about one annulus in length, but they lengthen somewhat abruptly over the distal one-third to form a noticeably penicillate tip (not like the conspicuous terminal brush, however, found in species of *Eliurus*). Notwithstanding the wide range in absolute lengths (Table 21-2), the hind feet of *Monticolomys* and *Macrotarsomys* have similar proportions (HFL about 26–28% of HBL).

HIND FOOT—The genera differ markedly in hind foot conformation, size and apportionment of the plantar pads, and distribution of pedal hairs. The pes of *Macrotarsomys* appears more svelte and absolutely narrower in view of the greater length of the proximal tarsal-metatarsal portion relative to the distal phalanges (Fig. 21-2). Not

only are the digits of *Macrotarsomys* generally shorter compared to those of *Monticolomys,* the outer members (I and V) are more reduced relative to the central three (II–IV), a proportional configuration evident in both the intact hind foot and the foot skeleton (Figs. 21-2 and 21-3). Thus, in *Macrotarsomys,* the claw of digit V extends to the junction of phalanges 1–2 of digit IV (junction of 2–3 in *Monticolomys*), and that of digit I reaches the end of the second metatarsal (middle of the first phalanx of digit II in *Monticolomys*). In addition, the five metatarsal bones in *Macrotarsomys* are closely appressed, although not fused, along their full length. Those of *Monticolomys,* however, splay noticeably at their distal ends and appear in looser contact along their proximal sections (Fig. 21-3).

Individuals of both *Monticolomys* and *Macrotarsomys* possess six plantar pads, but their size, shape, and spatial arrangement contrast appreciably. The six footpads in *Monticolomys* are fleshy, bulbous mounds, more of less equal to one another in circumference. In *Macrotarsomys,* the pads are not only smaller and lower in relief but differ in size; that is, the posterior three (thenar, hypothenar, and interdigital 1) are about half the diameter and protuberance of the anterior interdigitals 2–4 (Fig. 21-2). The hypothenar and interdigital 1 are coaligned in *Macrotarsomys* (more alternate in *Monticolomys*), and the thenar appears to be positioned more distally from the heel. Perhaps the most noticeable difference when examining the plantar surfaces of the two is the development of the thenar pad—an ovate, pillowy mound in *Monticolomys* compared to an insubstantial, circular papilla in species of *Macrotarsomys.*

In contrast to the naked plantar surface of *Monticolomys,* scattered hyaline hairs are found on the sole in examples of *Macrotarsomys bastardi,* as well as along the ventral surface of the distal phalanges (Fig. 21-2). In particular, a small cluster of hairs typically marks the midsole, between interdigital pads 2–4 and the paired hypothenar and interdigital 1. The single fluid specimen of *Macrotarsomys ingens* examined (USNM 328831) lacks such isolated hairs on the midsole but possesses them on the undersides of the toes. Unlike the hairs covering the dorsum of the foot, these plantar hairs seem stiffer, but neither they nor hairs on the phalangeal undersurfaces were detected in the two fluid specimens of *Monticolomys.* On the other hand, the ungual tufts, tussocks of hairs that emerge at the base of the claws, ap-

pear more profuse in individuals of *Monticolomys* (Fig. 21-2), arching over and beyond the tip of the claw (in both *Macrotarsomys,* reaching about one-half to three-quarters of claw length but not surpassing the tip).

CRANIUM AND MANDIBLE—The crania of *Monticolomys* and *Macrotarsomys* share many qualitative traits that convey a fundamental resemblance. Notable among these are moderately elongate incisive foramina (LIF 62–68% of LD); a flat, short, and wide palate with simple posterior palatine foramina; broad, shallow parapterygoid fossae and narrow mesopterygoid fossa with large sphenopalatine vacuities; absence of alisphenoid struts; size and form of temporal openings and well-defined hamular process; and presence of vascular foramina and osseous grooves indicative of a primitive carotid blood supply. They principally depart from one another in features of the interorbital region, configuration of the maxillary portion of the zygoma, and anatomy of the auditory bullae and surrounding area.

The interorbital region and braincase of both genera are smooth and gently contoured, devoid of pronounced temporal ridges or crests. Specimens of *Macrotarsomys bastardi,* however, possess an absolutely and relatively wider interorbit such that little of the orbital floor (top of maxillary) is visible from above. Also, they typically display a weak supraorbital shelf at the rear of the frontals that imparts a sharper constriction to the interorbit and longer appearance to the braincase (Fig. 21-4). The interorbit in examples of *Macrotarsomys ingens* has a relatively narrow, hourglass-shaped (amphoral) interorbit, more closely resembling that of *Monticolomys.*

The zygomatic plate in examples of *Monticolomys* is absolutely and relatively (BZP 8% of ONL) narrower than that observed in both species of *Macrotarsomys* (BZP 10% of ONL). Not only do specimens of *Macrotarsomys* have broader zygomatic plates, forming deeper zygomatic notches, but the zygomatic process of the maxilla widens appreciably at its union with the plate and has a more rugose surface (Fig. 21-7). A bony ledge from the lacrimal interrupts the anterodorsal perimeter of the orbit in samples of *Macrotarsomys bastardi* but not those of *Monticolomys* (Figs. 21-4 and 21-7). This tabular projection, reminiscent of the condition observed in certain Gerbillinae (Carleton, 1980), is intermediate in size in *M. ingens.*

Bullar inflation is pronounced in both species of *Macrotarsomys* (DAB about 48% of BBC)
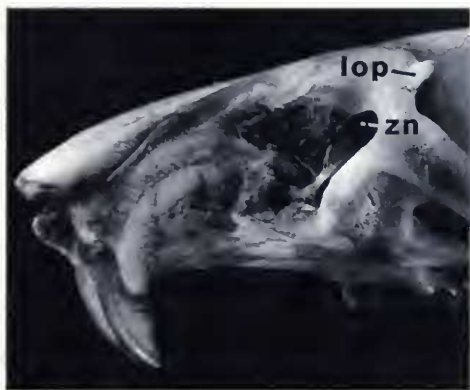
Fig. 21-7. Left lateral–oblique view of the rostrum and anterior zygomatic region: **top**, *Monticolomys koopmani* (FMNH 151899; Fianarantsoa Province, RNI d'Andringitra); **bottom**, *Macrotarsomys bastardi* (USNM 578715; Toliara Province, Petriky Forest). Abbreviations: lop, orbital projection of the lacrimal bone; pm, premaxilla; zn, zygomatic notch; zp, zygomatic plate. Note the wider zygomatic plate and deeper notch in *Macrotarsomys*, as well as the tabular extension of the lacrimal bone at the anterodorsal rim of the orbit.

less so in *Monticolomys* (DAB 37% of BBC), and perhaps accounts for certain other cranial dissimilarities. In *Macrotarsomys*, hypertrophy of the ectotympanic (Figs. 21-8 and 21-9), particularly noticeable in the expanse of translucent bone enclosing the middle ear cavity, plausibly relates to reduction of the middle lacerate foramen (present as a slit in *Monticolomys*), almost complete investiture of the periotic in ventral view (visible as posteromedial wedge in *Monticolomys*), and formation of a deep trough on the medial bullar wall for passage of the internal carotid artery (round foramen in *Monticolomys*). In both genera, the tegmen tympani, an anterior flange of the periotic

that roofs the epitympanic recess, lacks articulation with the squamosal, presumably an ancestral connection found in many New World muroids (see Voss, 1993) and in some nesomyines (e.g., *Eliurus*; see Carleton, 1994, Fig. 18). The tegmen tympani is inconspicuous though visible within the postglenoid foramen of *Monticolomys*, but it is smaller yet in *Macrotarsomys* and wholly obscured by the thickened, rugose dorsal rim of the external auditory meatus (Fig. 21-8).

Mandibular conformation of the two genera differs in several details. In *Monticolomys*, the coronoid process is more substantial and oriented more vertically; in contrast, the process in species of *Macrotarsomys* tapers to a thin spine that is angled more posterodorsally, in parallel to the orientation of the condylar process. As a consequence, the sigmoid notch of *Macrotarsomys* appears narrower and shallower (Fig. 21-4); that of *Monticolomys* forms a broader half-oval typical of many muroids. The angular notch in specimens of *Macrotarsomys* is deeply excavated, imparting a broader and longer definition to the angular and condylar processes. The concavity of the angular notch is shallower in *Monticolomys*, and the angular and condylar processes are normally proportioned.

DENTITION—The upper incisors of *Macrotarsomys*, like those of *Monticolomys*, lack enamel grooves but differ slightly in color; they are yellow-orange in the former and medium orange in the latter.

The molars of *Monticolomys* and *Macrotarsomys* are so remarkably alike that correct segregation of the genera is doubtful, except on the basis of size (Fig. 21-5). A trace of a posteroloph and minute posteroflexus is discernible on the M1-2s of most *Monticolomys* and *Macrotarsomys ingens*, but they seem to be lacking on those of *M. bastardi*, even for individuals with little tooth wear. The anteroconid is weakly defined in both genera, appearing as little more than an undifferentiated procingulum that originates from the anterolingual shoulder of the metaconid, forms the front rim of the tooth, and merges imperceptibly with the anterolabial cingulum near the protoconid. In some examples of *Macrotarsomys*, however, especially *M. ingens* (USNM 576753), a shallow indentation (vestige of the metaflexid?) on the anterolingual face of m1 imparts some separation of the metaconid from the presumptive anteroconid. Such evident differences must be viewed as qualified until verified by larger series of each species, including juveniles.
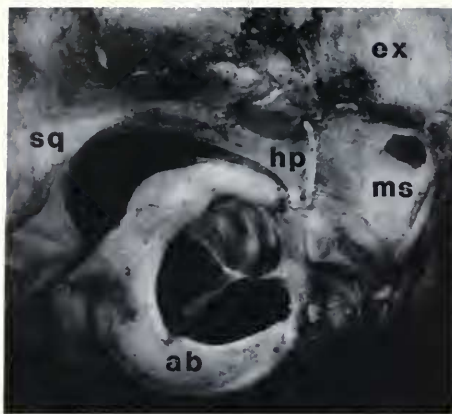
FIG. 21-8. Left lateral view of otic region and associated foramina: **left,** *Monticolomys koopmani* (FMNH 151900; Fianarantsoa Province, RNI d'Andringitra); **right,** *Macrotarsomys bastardi* (USNM 578717; Toliara Province, Petriky Forest). Abbreviations: ab, auditory bulla (ectotympanic); ex, exoccipital; hp, hamular process of the squamosal; ms, mastoid capsule of periotic; pgf, postglenoid foramen; sq, squamosal; ssf, subsquamosal fenestra; tt, tegmen tympani. The tegmen tympani fails to contact the squamosal in either genus, but it remains visible within the postglenoid foramen of *Monticolomys* and is obscured by the rugose dorsal rim of the ectotympanic in *Macrotarsomys*.

The Miocene Fossil *Protarsomys* Lavocat

The time of arrival of the first nesomyine, or nesomyines, into Madagascar remains inferential, given the absence of terrestrial Tertiary records on the island and the rarity of appropriately aged fossil muroids from sites in eastern Africa, the presumed area of origin. Lavocat (1978) postulated the entrance of ancestral nesomyines by over-water dispersal in the lower Miocene, in part because this epoch marks the first appearance of archaic cricetodontids in Africa. A period later than the lower to middle Miocene would prove difficult to reconcile with the lack of murines in Madagascar; they appear in the late Miocene of northern Africa and become commonplace in Pliocene beds of sub-Saharan Africa (see, e.g., Jacobs, 1985; Denys, 1987).

A more pivotal consideration, however, concerns the afrocricetodontine *Protarsomys macinnesi* (Muroidea: Cricetodontidae). Lavocat (1973) described this fossil rodent from the Rusinga Faunal Assemblage, lower Miocene of Kenya, and viewed (1978: p. 80) it as close to the ancestry of the Malagasy Nesomyinae, in particular *Macrotarsomys*: "The genus *Protarsomys*, approximately the size of recent *Mus musculus*, is so close to the Recent *Macrotarsomys* [his comparisons involved only *M. bastardi*, not the larger *M. ingens*] of Madagascar that one must evidently find in this *Protarsomys*, or in very close relatives of this ge-

nus, the ancestors of the Malagasy rodents." Chaline et al. (1977) had earlier formalized this interpretation by synonymizing *Protarsomys* under *Macrotarsomys*, an action and affinity reaffirmed by Petter (1990).

Description of *Monticolomys*, which itself exhibits traits suggesting relationship to *Macrotarsomys*, necessarily requires some consideration of Lavocat's (1973) *Protarsomys*. The remarkable holotype of *Protarsomys* (KNM 2350) consists of a mostly intact skull with associated lower jaws embedded in matrix. Partial removal of the encasing matrix has revealed the general dimensions and morphology of the cranium and mandibles in dorsal and lateral view, but features of the palate, basicranium, and otic capsules, as well as occlusal surfaces of the upper and lower molars, are still obscured on the type specimen. Accordingly, size comparisons of *Protarsomys* to specimens of *Monticolomys* and *Macrotarsomys* are limited to those variables accessible to measurement on the borrowed cast of the holotype. The configuration of other cranial and dental features has been gleaned from Lavocat's (1973) excellent description, from the cast of a referred lower right mandible with m1-3 (KNM 2188), and from inspection of his Plate 10, which portrays another attributed specimen (KNM 2353) in which the ventral surface of the skull is exposed.

As noted by Lavocat (1973, 1978), *Protarsomys* has a small skull, about the size of a house mouse, and as such, it is considerably smaller than

FIG. 21-9. Ventral view of left otic region and parapterygoid fossa: **left,** *Monticolomys koopmani* (FMNH 151900; Fianarantsoa Province, RNI d'Andringitra); **right,** *Macrotarsomys bastardi* (USNM 578717; Toliara Province, Petriky Forest). Abbreviations: ab, auditory bulla (ectotympanic); cc, carotid canal for passage of the internal carotid artery; iag, groove marking the course of the infraorbital branch of the stapedial artery; mf, mesopterygoid fossa; mlf, middle lacerate foramen; pac, posterior opening to the alisphenoid canal; ppf, parapterygoid fossa; sag, squamosal-alisphenoid groove, which indicates the presence of the supraorbital branch of the stapedial artery; sf, stapedial foramen. The middle lacerate foramen remains patent in *Monticolomys* but is ventrally obscured by the inflated ectotympanic bulla in *Macrotarsomys*.

individuals of either *Monticolomys* or *Macrotarsomys bastardi* (Table 21-3). Disparity in size, of course, is not relevant to generic membership, but the condition of other characters does bring into question the closeness of the purported phyletic affinity.

Lavocat (1973) stressed similarities in overall skull shape and curve of the cranial vault of his new genus *Protarsomys* and *Macrotarsomys*. They both agree, in a general way, in having a somewhat delicate rostrum, narrow zygomatic span, smoothly contoured braincase, and gently arched skull. Although not expanded laterally, the arches of *Protarsomys* over their midsection are notably stout for the size of the skull, heavier than those observed in the larger *Macrotarsomys*. The

comparatively broad interorbit and posteriorly divergent frontals in *Protarsomys* convey additional resemblance to the cranium of *Macrotarsomys bastardi*; however, possession of wide frontals that slightly overhang the rear of the orbit does not characterize the other living member of the genus, *M. ingens*.

Temporal fenestration and definition of a hamular process appear comparable in the fossil and the Recent genera, but the otic capsules of *Macrotarsomys* are substantially larger than those of *Protarsomys*. The inflation of the bullae of *Protarsomys* with respect to *Monticolomys* is difficult to ascertain because of the distorted preservation in this region, but they seem still smaller, to judge from the figured specimen (Lavocat, 1973: Plate

TABLE 21-3. Comparison of selected cranial dimensions (in mm) of the Miocene fossil *Protarsomys* (cast of holotype, KNM 2350) with recent *Monticolomys* (N = 4) and *Macrotarsomys* (N = 9). For the latter two taxa, the mean and range are given.

Variables	*Protarsomys macinnesi*	*Monticolomys koopmani*	*Macrotarsomys b. bastardi*
ONL	21.6	27.4 (26.3–28.1)	28.1 (26.7–28.9)
ZB	10.8	13.6 (13.1–14.1)	14.0 (13.0–14.6)
BBC	9.3	12.7 (12.4–13.2)	11.3 (10.9–11.5)
IOB	3.7	3.9 (3.9–4.0)	4.6 (4.3–4.7)
LR	7.3	9.5 (8.5–10.2)	10.2 (9.5–11.1)
BR	4.1	4.5 (4.2–4.9)	4.7 (4.4–5.1)
LD	5.6	7.7 (7.2–8.0)	7.4 (6.8–8.0)
BM1s	4.4	5.9 (5.7–6.0)	5.9 (5.5–6.2)
BZP	2.0	2.2 (2.1–2.2)	2.9 (2.6–3.1)

10). Lavocat identified a stapedial foramen and carotid canal in *Protarsomys*; the presence of other cranial foramina and placement of vascular tracings indicative of the carotid circulatory plan are unknown. The incisive foramina are moderately long and wide, as in *Macrotarsomys* and *Monticolomys,* and they terminate posteriorly near the level of the anterior roots of the M1s.

Protarsomys contrasts strikingly with *Macrotarsomys* and *Monticolomys* in the architecture of its infraorbital canal and accompanying zygomatic plate. The infraorbital foramen of *Protarsomys* is broadly elliptical or nearly circular. That observed in *Monticolomys* and *Macrotarsomys* recalls the oval "keyhole shape" typical of more derived muroids; that is, the ventral portion is narrowed as a neurovascular fissure relative to the spacious dorsal section, which is rounded for passage of the anterior body of the masseter medialis.

Presumably correlated with the different design of the infraorbital foramen is the construction of the zygomatic plate. In *Protarsomys,* the plate is small, about as long as wide, and marginally inclined above the horizontal; the front edge of the plate extends little beyond the superior ramus of the anterior zygomatic arch and defines only a shallow zygomatic notch. The zygomatic plate in examples of *Monticolomys* and *Macrotarsomys* occupies a greater area, clearly longer (taller dorsad) than wider, and angles noticeably oblique (dorsolaterad) to the midsagittal plane of the skull; the leading margin of the plate is produced farther forward, more so in *Macrotarsomys* than in *Monticolomys,* creating a deeper zygomatic notch. Relative to the molar rows, the zygomatic plate

of *Protarsomys* appears displaced posteriad, its rear edge coaligned with the anterior root of M1, a condition that Lavocat (1973) interpreted as plesiomorphic. In contrast, the plates in *Monticolomys* and *Macrotarsomys* are positioned further forward on the rostrum, well in advance of the front of the M1s.

We emphasize that the infraorbital foramen of *Monticolomys* and *Macrotarsomys,* compared to many murids and some nesomyines, forms a fairly broad oval that lacks pronounced compression of the ventral space as a narrow slit distinct from a much wider dorsal opening. Nevertheless, the infraorbital-zygomatic construction of these two genera more strongly suggests the typical murid condition. The round infraorbital canal and rudimentary, almost horizontal zygomatic plate of *Protarsomys,* on the other hand, resemble the development found in other contemporaneous Miocene Afrocricetodontinae, such as *Afrocricetodon* and *Notocricetodon* (Lavocat, 1973).

Lavocat (1973) noted two principal differences between the mandibles of *Protarsomys* and *Macrotarsomys.* No lateral protuberance marks the posterior limit of the alveolus of the lower incisor in *Protarsomys,* whereas a small but distinct capsular process occurs on the ascending ramus of *Macrotarsomys* (including *M. ingens* and *Monticolomys*). Furthermore, the apex of the masseteric crest in *Protarsomys* reaches only as far forward as below the middle of m1; in *Macrotarsomys* and *Monticolomys,* the crest passes beyond the anterior root of m1 to end just behind the mental foramen.

All three genera possess opisthodont upper incisors and very low-crowned, cuspate molars that retain longitudinal enamel connections (mures and murids). Their dentitions contrast substantially in other particulars. The molar tubercles in examples of *Macrotarsomys* and *Monticolomys* are relatively thickly enameled, their borders rounded, and their occlusal topography bunodont. Corresponding to the robust cusp development, the enamel folds and valleys appear narrower and more crevice-like. In *Protarsomys,* the principal cusps are less massive, forming tapered conical peaks, the enamel seemingly thinner (Lavocat [1973] characterized their form as pinched anteriorly-posteriorly or somewhat selenodont); the valleys between major cones are more open and their bottoms U-shaped. The anterocone of M1 forms a broad, occasionally bilobed cusp in *Macrotarsomys* and *Monticolomys;* that of *Protarsomys* is narrower, without suggestion of an an-

teromedian sulcus or bilobation. An anteroconid is weakly expressed in all three taxa, but that of *Protarsomys* is physically discrete, a distinct metaflexid, equal in size to the contralateral protoflexid, incising its posteromedial margin from the nearby metaconid. Posterolophs and companion posteroflexi are eminently discernible on the M1-2s of *Protarsomys*; these enamel features are imperfectly expressed or vestigial in specimens of *Macrotarsomys* and *Monticolomys*. The upper and lower third molars of *Protarsomys* are larger relative to the length of the toothrow. In particular, the m3 of the Miocene fossil exhibits a small but distinct entoconid, posterolophid, and posteroflexid—features that are indistinct or lost on the reduced m3 talonids of *Macrotarsomys* and *Monticolomys*. Finally, paramount among the dental structures mentioned by Lavocat (1973) *Protarsomys* displays low and thin mesolophs(ids) on its first two molars of the upper and lower toothrows. Such transverse enamel ridges do not occur in individuals of the two living genera.

Discussion

Comments on genealogical relations and historical biogeography of *Monticolomys* are necessarily preliminary in nature, a caveat that underscores the meager number of specimens and field data as yet available for fuller appreciation of its morphology, ecology, and geographical distribution. Small sample sizes, for instance, hinder definitive characterization of dental structures and recognition of qualitative differences, if they exist, between *Monticolomys* and species of *Macrotarsomys*. Treatment of their relationship within a rigorous context is hampered by the lack of resolution surrounding our understanding of higher-level phylogeny within Muroidea and, most important for our topic, the corroboration of Nesomyinae as monophyletic and a working hypothesis of generic interrelationships. In view of these uncertainties, the formal diagnosis of *Monticolomys* was broadly stated with reference to all seven other nesomyine genera. Those diagnostic characters, as well as others mentioned below, and the rationale for their polarity are elaborated by Hershkovitz (1962), Bugge (1970), Carleton (1980, 1994), Voss (1988, 1993), and Carleton and Musser (1989).

Relationships

The extant species of Neosomyinae have long been arranged in only seven genera, each one highly distinctive and all remarkable for the extreme scope of intergeneric morphological divergence (Ellerman, 1941; Petter, 1972; Carleton & Musser, 1984). The striking variety of Madagascar's native rodents is attested by the various comparisons drawn, albeit not always fittingly, to their outward appearances—the genera being likened to rabbits (*Hypogeomys*), gerbils (*Macrotarsomys*), voles (*Brachyuromys*), Old World murines (*Gymnuromys*), or generalized cricetines (*Nesomys*). Just as remarkably, the seven genera were thought, until recently, to contain among them just ten species (Petter, 1975; Honacki et al., 1982; Rakotondravony, 1987; Corbet & Hill, 1991). However, the portrayal of Madagascar's endemic rodents as depauperate is, at least in part, a specious conclusion based on inadequate biological survey and uncritical taxonomic study (see Carleton & Schmidt, 1990). The number of species acknowledged based on recent taxonomic revisions totals 16 (Musser & Carleton, 1993; Carleton, 1994), and now 17, with the diagnosis of *Monticolomys koopmani. Macrotarsomys*, named by Milne Edwards and Grandidier (1898) almost a century ago, was the last nesomyine genus heretofore described.

The existence of a few strongly differentiated genera (seven) embracing nearly as few species (ten), as the Malagasy rodents were so long understood, certainly influenced Ellerman's (1941, 1949) systematic treatment of the Nesomyinae. Indeed, Ellerman dismissed the evolutionary reality of the subfamily and redistributed the genera among five family-group taxa, several of them described as new within an inclusive Family Muridae: Arvicolinae, Brachytarsomyes (*Brachytarsomys*); Cricetinae (*Hypogeomys, Macrotarsomys,* and *Nesomys*); Gymnuromyinae (*Gymnuromys*); Murinae, Eliuri (*Eliurus*); and Tachyoryctinae, Brachyuromyes (*Brachyuromys*). His taxonomy controverted the conventional viewpoint on nesomyines—that is, a monophyletic group arising from a single immigrant stock and subsequently radiating in isolation (e.g., as classically narrated by Simpson, 1945)—but in doing so, he did cite characters and provide diagnoses for his reclassifications. Ellerman's (1941, 1949) ideas have yet to be seriously challenged as an alternative to the traditional arrangement.

The characterization of *Monticolomys,* howev-

er, departs from the prevalent pattern of extreme morphological differentiation and obscure kinship alliances so far apparent among nesomyine genera. That is to say, several cranial and dental characters clearly implicate a sister-group relationship between the new genus and a previously described form, namely *Macrotarsomys,* suggesting that the two share a more recent common ancestor relative to the cladogenesis of the six other nesomyine genera. Possible synapomorphies include reduction of the tegmen tympani and subsequent loss of contact with the squamosal, loss of the alisphenoid struts, marginal definition of the posterolophs, absence of mesolophs(ids), and a comparable degree of reduction of the upper and lower third molars.

To be sure, many more resemblances of *Monticolomys* and *Macrotarsomys* involve traits that are plausibly considered as primitive or those whose evolutionary polarity is equivocal. Among these are: size and extent of the incisive foramina; ovate infraorbital canal; forward position and dorsolateral orientation of the zygomatic plate; short, simple palate unmarked by corrugations or posterolateral palatal pits; wide, shallow parapterygoid fossae; mesopterygoid fossa comparatively narrow, perforated by spacious sphenopalatine vacuities; postglenoid and subsquamosal foramina present, defining a slender hamular process; smooth braincase without beading and ridging; a primitive orbitofacial blood supply (presence of vascular grooves across squamosal-alisphenoid and pterygoid; sphenofrontal and stapedial foramina patent); and development of a capsular process on the dentary. Dental similarities between the two genera are equally finely molded: toothrows anteriorly divergent; low molar crowns and bunodont form of their cusps; cusp position and retention of interconnecting, low-relief mures(ids); undivided anterocone; indistinct formation of an anteroconid and the virtual absence of a metaflexid contrasted to the deep protoflexid; and the number of roots on the molars.

Considered by themselves, the few derived character states may seem insufficient to posit sister-group stature between *Monticolomys* and *Macrotarsomys.* Nor, we acknowledge, are most or any of these character-state transformations, as articulated, unique within Muroidea. At the same time, and notwithstanding the weakness of inferring kinship on the basis of shared plesiomorphies, one cannot help but be impressed by the utter exactitude and number of their presumably ancestral resemblances. In weighing the five syn-

apomorphic features against the otherwise fundamental likeness of the genera in so many aspects of their craniodental morphology, we believe that a hypothesis of cognate affinity warrants attention at this formative stage of phylogenetic understanding among nesomyines (Fig. 21-10).

Sharply countershaded and bright pelage colors, silky fur texture, large pinnae, elongate pes, penicillate tail, and moderately inflated bullae are some of the superficial resemblances that have earned *Macrotarsomys* the sobriquet of the Madagascar gerbil (for instance, Webb, 1954). Among nesomyines, both *M. bastardi* Milne Edwards and Grandidier (1898) and *M. ingens* Petter (1959) possess these characteristics and other derived features that suggest their close kinship and vindicate their union in the genus *Macrotarsomys* (Fig. 21-10).

The muted pelage tones with agouti-banded ventral hairs, broader hind foot and relatively long lateral digits, well-developed ungual tufts, and conformation of the plantar pads in *Monitcolomys* suggest the physique of a scansorial forest-dweller. Such characteristics provide substantial external contrast to species of *Macrotarsomys,* in addition to cranial differences in the anterior xygomatic region and auditory bullae (Fig. 21-10). Accordingly, the diagnostic traits we have advanced for *Monticolomys* are unique in combination and make its recognition unambiguous. Nevertheless, among the characters surveyed, the identification of wholly autapomorphic features that define *Monticolomys* is less clear-cut.

The apparent lack of uniquely derived character states poses the question of whether the construction of *Monticolomys* is paraphyletic with regard to *Macrotarsomys.* Other than acknowledging the issue, a firm answer cannot be immediately or simply mustered without undertaking a detailed phylogenetic review of Nesomyinae. We are persuaded, nonetheless, that generic isolation of *Monticolomys koopmani* is both a reasonable taxonomic hypothesis at this stage of investigation and a defensible one, as based on the number and kinds of morphological differences so far uncovered that set it apart from *Macrotarsomys* (Fig. 21-10). In this regard, the amount of anagenetic change that distinguishes *M. koopmani* from species of *Macrotarsomys* far surpasses that observed within other genera (such as *Eliurus* and *Nesomys*) that contain different species inhabiting dry western versus humid eastern biomes of Madagascar (Carleton, 1994, and unpubl. data). Morphologically and ecologically, *Monticolomys* ex-
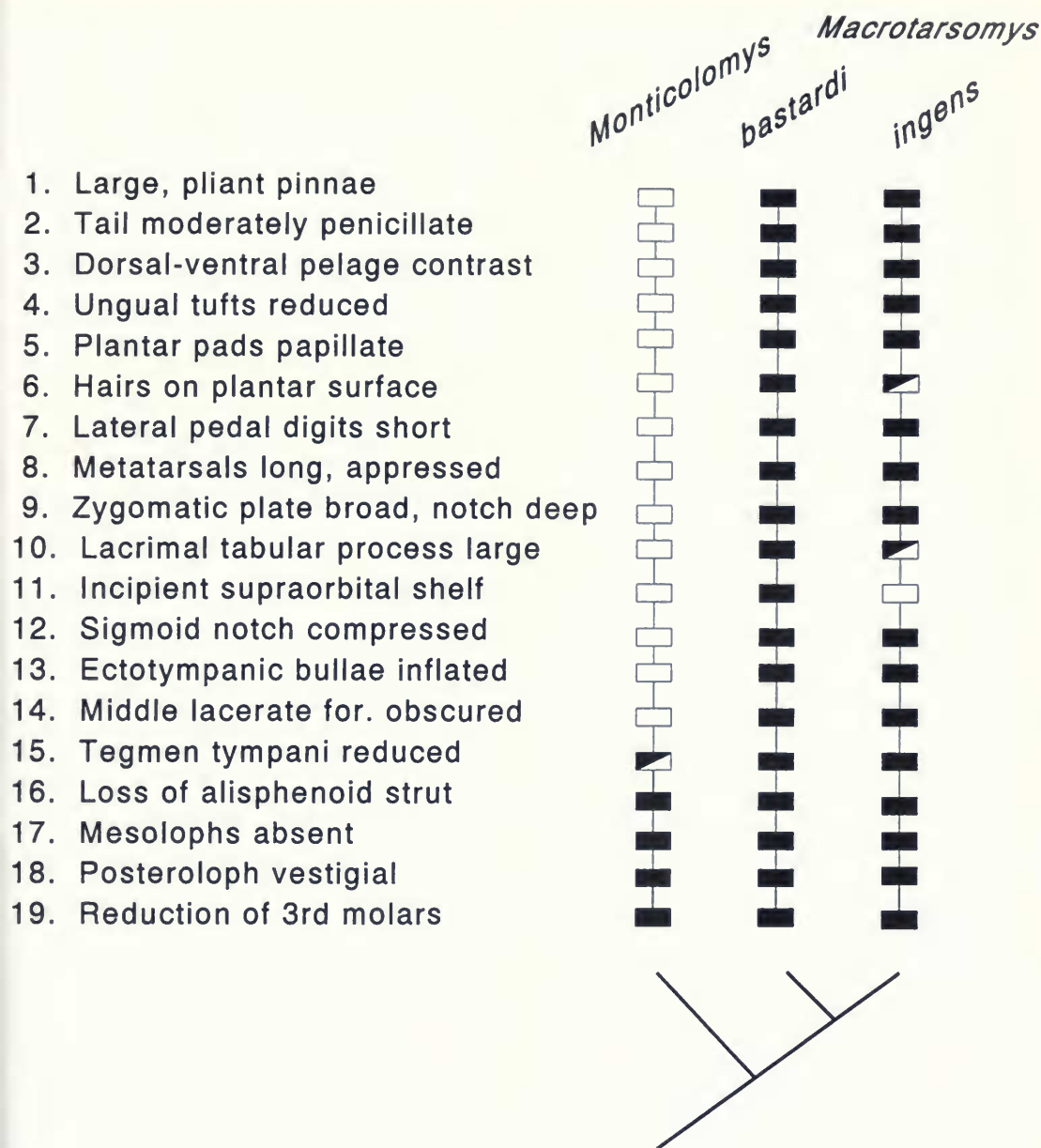
Monticolomys   Macrotarsomys
                bastardi   ingens

1. Large, pliant pinnae
2. Tail moderately penicillate
3. Dorsal-ventral pelage contrast
4. Ungual tufts reduced
5. Plantar pads papillate
6. Hairs on plantar surface
7. Lateral pedal digits short
8. Metatarsals long, appressed
9. Zygomatic plate broad, notch deep
10. Lacrimal tabular process large
11. Incipient supraorbital shelf
12. Sigmoid notch compressed
13. Ectotympanic bullae inflated
14. Middle lacerate for. obscured
15. Tegmen tympani reduced
16. Loss of alisphenoid strut
17. Mesolophs absent
18. Posteroloph vestigial
19. Reduction of 3rd molars

FIG. 21-10. Distribution of presumptive synapomorphies (solid rectangles) and hypothesized cladistic relationship between *Monticolomys koopmani* and species of *Macrotarsomys*. Half-filled rectangles denote intermediate character states.

hibits many of the characteristics that one might postulate for an ancestor to *Macrotarsomys*. The generic validity of *Monticolomys* and its proposed relationship to *Macrotarsomys* should be subjected to expanded character analyses and cladistic scrutiny, drawing upon representatives of all nesomyine genera as well as other intelligently selected outgroups within Muroidea, and assimilating information from additional anatomical systems, karyology, and genetics.

Whatever the outcome of such future phylogenetic investigation, characteristics of the Miocene form *Protarsomys*, as reviewed herein, subvert neither the definition of *Monticolomys* nor the

recognition of *Macrotarsomys* as a genus apart. Many resemblances between *Protarsomys* and *Macrotarsomys* that so impressed Lavocat (1973) are aspects of shape and form, features that do not simply lend themselves to formulation of character states and argument of polarity. Other general likenesses—for instance, a brachyodont dentition, presence of mures(ids), and a rudimentary anteroconid—are plausibly interpreted as shared primitive conditions that do not necessarily provide support for their close relationship. Moreover, the strict anatomical correspondence of similarities so generally stated is less persuasive when examined in detail (such as anteroconid formation and cuspate topography of the brachyodont crown). When comparison is restricted to qualitative characters, one is struck more by the many and ample dissimilarities: configuration of the infrarorbital canal; size, position, and orientation of the zygomatic plate; inflation of the auditory bullae; formation of the anteroconid and definition of the metaflexid; occurrence of mesolophs and mesolophids, posterolophs and posteroflexi; and degree of reduction of the third molars. The union of the fossil species *Protarsomys macinnesi* Lavocat (1973) with recent *Macrotarsomys* species cannot be construed on such profound differences and the want of any contravening synapomorphic traits.

Lavocat (1973, 1978), it should be underscored, did not himself advocate the synonymy of *Protarsomys* under *Macrotarsomys*. That action was promulgated by Chaline et al. (1977) and reiterated by Petter (1990), without discussion of character data justifying the new combination. Instead, Lavocat (1973, 1978) drew attention to their likenesses and proposed the descent of Nesomyinae from a Miocene, eastern African form such as *Protarsomys*. He retained the latter as a genus of Afrocricetodontinae, Family Cricetodontidae, set apart from a broadly defined Family Nesomyidae, in which he included Nesomyinae and several other archaic African groups (see comments in Carleton & Musser, 1984). In arguing against the generic equivalency of *Protarsomys* and *Macrotarsomys,* we do not necessarily discount Lavocat's (1973, 1978) basic thesis with respect to the taxonomic and geographical origin of nesomyines, yet neither can we, at this stage, identify persuasive character information that would support it.

Like other early Miocene muroids, *Protarsomys* displays a somewhat generalized morphology, but from such evidence, one can argue no

more strongly for its phyletic association with nesomyines than with another African group such as the petromyscines. Continued exploration of Tertiary fossil sites in eastern Africa may disclose new cricetodontids whose relationship to nesomyines is incontestable. The discovery of relevant Miocene–Pliocene fossils in Madagascar remains a possibility. Fresh examination of the original type series of *Protarsomys* could feasibly reveal new characters that would bear critically on the question of its relationship to nesomyines. The problem is addressable and amenable to improved resolution.

Biogeography

In a phytogeographic classification of the floral associations of Madagascar, Humbert (1955) recognized a unique High Mountain Domain that occurs patchily on a few isolated peaks between Andohohela in the south and Tsaratanana in the north. Two of the mountaintop communities falling within this domain are found on the massifs of Ankaratra and Andringitra. Upper montane forests (above approximately 1500 m) on these two massifs, particularly in the zone just below the tree line, share many endemic sclerophyllous plants, principally members of the family Ericaceae (Koechlin, 1972; Koechlin et al., 1974). Furthermore, the fragmented distributions of numerous animal species—including, for example, terrestrial insects (Paulian, 1961), aquatic insects (Chapter 9, this work), and several amphibians and reptiles (Chapter 17)—are restricted to the upper reaches of these central and south-central highlands. So far as is currently known, the distributional pattern of the nesomyine rodent *Monticolomys koopmani* also conforms to Humbert's (1955) High Mountain Domain (Fig. 21-11).

The present-day discontinuity in the ranges of all these organisms and the reiterative pattern of vicariance strongly indicate that a corridor of upper montane vegetation once connected the summits of Ankaratra and Andringitra. On the basis of modern topography, feasible links between these two massifs may have occurred along the Fianarantsoa Plateau, between 1000 and 1300 m, and through the Ambalavao Pass, between 800 and 1000 m (Raxworthy & Nussbaum, in press). Thus, depression of upper montane zones to as low as 1000 m would have been necessary in order for animals such as *Monticolomys* to become
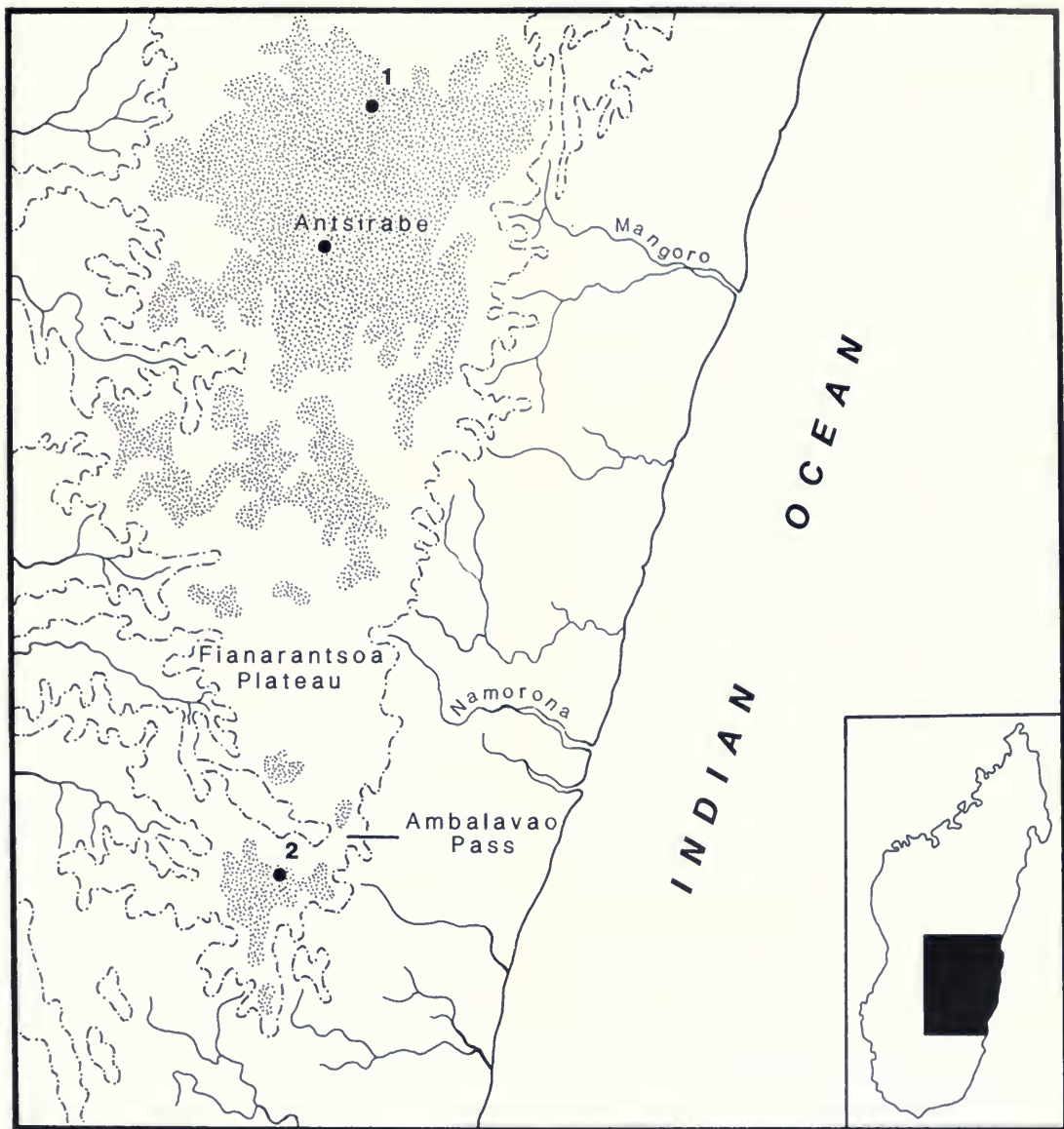
FIG. 21-11. Southeastern sector of Madagascar's Central High Plateau with reference to the two known geographic occurrences of *Monticolomys koopmani*: **1**) Manjakatompo, about 19°20′S 47°26′E; **2**) 38 km S Ambalavao, RNI d'Andringitra, 22°11′S 46°58′E. Stippled areas indicate uplands above 1500 m; this elevation approximates the present-day lower boundary of upper montane vegetation. The dot-and-dashed line corresponds to the 1000-m contour, the hypothesized lowest depression of the upper montane-sclerophyllous zone during the Holocene (see the Discussion section).

distributed continuously over these mountains (Fig. 21-11).

Evidence for cooler periods and consequent lowering of vegetation zones is available for the Quaternary, when Madagascar experienced cyclical climatic shifts (Burney, in press). Pollen cores

from Lake Tritrivakely, near Antsirabe (80 km S Ankaratra and 250 km N Andringitra) on the Central Plateau (Fig. 21-11), reveal considerable variation in the natural vegetational communities of the area over the past 36,000 years (Burney, 1987; Gasse et al., 1994). During both the Pleistocene

and early Holocene, ericaceous pollen generally accounted for over 50% of the taxa deposited in the lacustrine sediments, but after the middle Holocene this proportion dropped to between 0 and 30%. During portions of the Quaternary, high mountain floral communities likely descended to approximately 1000 m (Burney, in press), an elevation sufficiently low for upper montane forest and sclerophyllous vegetation to have extended between the regions of Ankaratra and Andringitra. Some time in the middle Holocene, the upper montane and sclerophyllous floras retreated to the uppermost slopes of the mountains and severed the geographic ranges of animals dependent on such habitats.

In summary, information derived from palynology and from the congruent distributions of other plants and animals convincingly explains the present-day vicariant occurrence of *Monticolomys koopmani* on the Andringitra and Ankaratra massifs. Specimen-based documentation of nesomyine distributions, in general poor over much of Madagascar, is almost nonexistent for the island's high mountain zones, particularly those on such huge mountain systems as Tsaratanana and Marojejy in the north and Andohohela in the south. Whether the distributions of other nesomyine rodents repeat a similar geographic pattern is therefore uncertain, but *Eliurus majori,* as its broken range is currently understood, is a possible candidate (see Carleton, 1994; and Chapter 22, this work).

Note added in proof

Monticolomys koopmani still occurs on the Ankaratra Massif. During a biological inventory of the Forêt de Nosiarivo (2000 m) in February 1996, conducted by S. M. Goodman and D. Rakotondravony, a specimen of *Monticolomys koopmani* was captured (FMNH 156211). The animal was trapped on the ground and in degraded habitat close to the forest edge.

Acknowledgments

Literature Cited

ARCHBOLD, R. 1932. A new lemur from Madagascar. American Museum Novitates, **518:** 1.

BUGGE, J. 1970. The contribution of the stapedial artery to the cephalic arterial supply in muroid rodents. Acta Anatomica, **76:** 313–336.

BURNEY, D. A. 1987. Pre-settlement vegetation changes at Lake Tritrivakely, Madagascar. Palaeoecology of Africa, **18:** 357–381.

———. In press. Theories and facts regarding Holocene environmental change before and after human colonization. *In* Goodman, S. M., and B. D. Patterson, eds., Natural and Human-Induced Change in Madagascar. Smithsonian Institution Press, Washington, D.C.

CARLETON, M. D. 1980. Phylogenetic relationships in neotomine–peromyscine rodents (Muroidea) and a reappraisal of the dichotomy within New World Cricetinae. Miscellaneous Publications of the Museum of Zoology, University of Michigan, **157:** 1–146.

———. 1994. Systematic studies of Madagascar's endemic rodents (Muroidea: Nesomyinae): Revision of the genus *Eliurus.* American Museum Novitates, **3087:** 1–55.

CARLETON, M. D., AND G. G. MUSSER. 1984. Muroid rodents, pp. 289–379. *In* Anderson, S., and J. K. Jones, Jr., eds., Orders and Families of Recent Mammals of the World. John Wiley and Sons, New York, 686 pp.

———. 1989. Systematic studies of oryzomyine rodents (Muridae, Sigmodontinae): A synopsis of *Microryzomys.* Bulletin of the American Museum of Natural History, **191:** 1–83.

CARLETON, M. D., AND D. F. SCHMIDT. 1990. Systematic studies of Madagascar's endemic rodents (Muroidea: Nesomyinae): An annotated gazetteer of collecting localities of known forms. American Museum Novitates, **2987:** 1–36.

CHALINE, J., P. MEIN, AND F. PETTER. 1977. Les grandes lignes d'une classification évolutive des Muroidea. Mammalia, **41:** 245–252.

CORBET, G. B., AND J. E. HILL. 1991. A World List of Mammalian Species, 3rd edition. Natural History Museum Publications, London, vii+243 pp.

DELACOUR, M. J. 1932. Les oiseaux de la Mission Zoologique Franco-Anglo-Américaine à Madagascar. L'Oiseau et la Revue de Francaise d'Ornithologie, nouvelle serie, **2**: 1–96.

DENYS, C. 1987. Rodentia and Lagomorpha, pp. 118–170. *In* Leakey, M. D., and J. H. Harris, eds., Laetoli, a Pliocene site in Tanzania. University of Oxford Press, London.

ELLERMAN, J. R. 1941. The Families and Genera of Living Rodents. Volume 2, Family Muridae. London: British Museum (Natural History), xii+690 pp.

———. 1949. The Families and Genera of Living Rodents. Volume 3, Appendix II [Notes on the rodents from Madagascar in the British Museum, and on a collection from the island obtained by M. C. S. Webb]. London: British Museum (Natural History), v+210 pp.

GASSE, F., E. CORTIJO, J.-R. DISNAR, L. FERRY, E. GILBERT, C. KISSEL, F. LAGGOUN-DEFARGE, E. LALLIER-VERGES, J.-C. MISKOVSKY, B. RATSIMBAZAFY, F. RANAIVO, L. ROBISON, P. TUCHOLKA, J.-L. SAOS, A. SIFFEDINE, M. TAIEB, E. VAN CAMPO, AND D. WILLIAMSON. 1994. A 36 ka environmental record in the southern tropics: Lake Tritrivakely (Madagascar). Comptes rendus de l'Académie des Sciences, série II, **318**: 1513–1519.

HERSHKOVITZ, P. 1962. Evolution of Neotropical cricetine rodents (Muridae) with special reference to the phyllotine group. Fieldiana, Zoology, **46**: 1–524.

HONACKI, J. H., K. E. KINMAN, AND J. W. KOEPPL. 1982. Mammal Species of the World. Allen Press and the Association of Systematics Collections, Kansas, ix+694 pp.

HUMBERT, H. 1955. Les térritores phytogéographiques de Madagascar. Leur cartogarphie. Année Biologique, série III, **31**(5–6): 195–204.

JACOBS, L. L. 1985. The beginning of the age of murids in Africa. Acta Zoologica Fennica, **170**: 149–151.

KOECHLIN, J. 1972. Flora and vegetation of Madagascar, pp. 145–190. *In* Battistini, R., and G. Richard-Vindard, eds., Biogeography and Ecology in Madagascar. W. Junk, The Hague, xv+765 pp.

KOECHLIN, J., J.-L. GUILLAUMET, AND P. MORAT. 1974. Flore et végétation de Madagascar. J. Kramer, Vaduz, Germany.

LAVOCAT, R. 1973. Les rongeurs du Miocène d'Afrique Orientale. I. Miocène inférieur. Mémoires et Travaux de l'Ecole Pratique des Hautes Etudes, Institute de Montpellier, **1**: 1–284.

———. 1978. Rodentia and Lagomorpha, pp. 69–89. *In* Maglio, J. V., and H. B. S. Cooke, eds., Evolution of African Mammals. Harvard University Press, Cambridge, ix+641 pp.

MILNE-EDWARDS, A., AND G. GRANDIDIER. 1898. Description d'une espèce nouvelle de Muridé provenant de Madagascar. Bulletin de Muséum National d'Historie Naturelle, serie 1, **4**: 179–181.

MUSSER, G. G., AND M. D. CARLETON. 1993. Family Muridae, pp. 501–755. *In* Wilson, D. E., and D. M. Reeder, eds., Mammal Species of the World: A Taxonomic and Geographic Reference, 2nd edition. Smithsonian Institution Press, Washington, D.C., xviii+1207 pp.

NICOLL, M. E., AND O. LANGRAND. 1989. Madagascar: Revue de la conservation et des Aires Protégées. World Wide Fund for Nature, Gland, Switzerland, xvii+374 pp.

PAULIAN, R. 1961. La zoogéographie de Madagascar et des iles voisines. Faune de Madagascar, **13**: 1–484.

PERRIER DE LA BÂTHIE, H. 1927. Le Tsaratanana, l'Ankaratra, et l'Andringitra. Mémoire de l'Academie Malgache, **3**: 1–68.

PETERS, W. 1870. Uber *Nesomys rufus,* eine neue gattung und art madagascarischer nager. Sitzungs-Berichte der Gesellschaft naturforsender Freunde, Berlin, **1870**: 54–55.

PETTER, F. 1959. Un nouveau rongeur de Madagascar (Nesomyinae): *Macrotarsomys ingens* nov. sp. Mammalia, **23**: 139–148.

———. 1972. The rodents of Madagascar: The seven genera of Malagasy rodents, pp. 661–665. *In* Battistini, R., and G. Richard-Vindard, eds., Biogeography and Ecology in Madagascar. W. Junk, The Hague, xv+765 pp.

———. 1975. Family Cricetidae: Subfamily Nesomyinae. Part 6.2, pp. 1–4. *In* Meester, J., and H. W. Setzer, eds., The Mammals of Africa: An Identification Manual. Smithsonian Institution Press, Washington, D.C.

———. 1990. Relations de parenté des rongeurs de Madagascar. Accademie Nazionale dei Lincei, Atti dei Convegni Lincei, **85**: 829–837.

RAKOTONDRAVONY, D. A. 1987. Les rongeurs à Madagascar, pp. 93–94. *In* Mittermeier, R. A., L. H. Rakotovao, V. Randrianasolo, E. J. Sterling, and D. Devitre, eds., Priorités en matière de conservation des espèces à Madagascar. IUCN, Gland, Switzerland, 167 pp.

RAND, A. L. 1932. Mission Franco-Anglo-Américaine à Madagascar. Notes de voyage. L'Oiseau et la Revue de Francaise d'Ornithologie, nouvelle serie, **2**: 227–282.

———. 1935. On the habits of some Madagascar mammals. Journal of Mammalogy, **16**: 89–104.

———. 1936. The distribution and habits of Madagascar birds. A summary of the field notes of the Mission Zoologique Franco-Anglo-Américaine à Madagascar. Bulletin of the American Museum of Natural History, **72**: 143–499.

RAXWORTHY, C. J., AND R. A. NUSSBAUM. In press. Zoogeographic patterns of reptile endemicity and vicariance in eastern Madagascar. *In* Goodman, S. M., and B. D. Patterson, eds., Natural and Human-Induced Change in Madagascar. Smithsonian Institution Press, Washington, D.C.

REIG, O. A. 1977. A proposed unified nomenclature for the enamelled components of the molar teeth of the Cricetidae (Rodentia). Journal of Zoology, London, **181**: 227–241.

SIMPSON, G. G. 1945. The principles of classification and a classification of mammals. Bulletin of the American Museum of Natural History, **85**: 1–350.

UNITED STATES BOARD ON GEOGRAPHIC NAMES. 1989.

Gazetteer of Madagascar, 2nd edition. Defense Mapping Agency, Washington, D.C., xvii+826 pp.

Voss, R. S. 1988. Systematics and ecology of ichthyomyine rodents (Muroidea): Patterns of morphological evolution in a small adaptive radiation. Bulletin of the American Museum of Natural History, **188:** 259–493.

———. 1993. A revision of the Brazilian muroid rodent genus *Delomys* with remarks on "thomasomyine" characters. American Museum Novitates, **3073:** 1–44.

Voss, R. S., and L. F. Marcus. 1992. Morphological evolution in muroid rodents: II. Craniometric factor divergence in seven Neotropical genera, with experimental results from *Zygodontomys*. Evolution, **46:** 1918–1934.

Webb, C. S. 1954. The odyssey of an animal collector. Longmans, London, xv+368 pp.